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# TRENDS AND OCEANOGRAPHIC CORRELATES OF PINNIPED POPULATIONS IN THE GULF OF THE FARALLONES, CALIFORNIA

By

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ADMINISTRATIVE REPORT LJ-97-02C

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# TRENDS AND OCEANOGRAPHIC CORRELATES OF PINNIPED POPULATIONS IN THE GULF OF THE FARALLONES, CALIFORNIA

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Final Report

to

National Marine Fisheries Service
Southwest Fisheries Science Center

**FEBRUARY 1997**

(Key words: pinniped population dynamics, central California, oceanographic conditions.)

**ADMINISTRATIVE REPORT LJ-97-2C**

This report was prepared by Bill Sydeman and Sarah Allen under contract No. 40JGNF500431 from the National Marine Fisheries Service, Southwest Fisheries Science Center, 8604 La Jolla Shores Dr., La Jolla, CA 92037-1508. The statements, findings, conclusions and recommendations herein are those of the author and do not necessarily reflect the views of the National Marine Fisheries Service. Mark Lowry of the Southwest Fisheries Science Center served as Contract Officer's Technical Representative for this contract.

## ABSTRACT

We surveyed pinnipeds (California and northern sea lion and harbor and northern elephant seal) populations at the South Farallon Islands (SFI) and Point Reyes (PR), central California, from 1973 to 1994, and correlated abundance estimates with oceanographic conditions. California sea lions increased over the study period, with peak numbers observed during and after the El Niño Southern Oscillation events of 1983 and 1992. Northern sea lions decreased at the SFI. Conservation issues include chemical contaminants (DDE, PCBs, Hg, and Se), diseases, possible competition with commercial fisheries (e.g. for Pacific hake; *Merluccius productus*), long-term changes in prey base (which may be related to oceanic warming), and demographic stochasticity. Harbor seals increased at both sites during the study period. Harbor seals were more abundant offshore (at the SFI) during years of relatively warm water, which may be related to their inability to find sufficient prey in coastal waters under these conditions. Northern elephant seal abundance at the SFI increased over the study period; however, the population size and productivity of breeding females at the SFI has decreased significantly in recent years. The decline in natality at the SFI has not been reflected in maximum haul-out numbers which are stable, and have been so since 1978. At PR, northern elephant seal population size and productivity has increased constantly since 1981. The short-term prognosis for pinniped populations, with the exception of the northern sea lion, in the Gulf of the Farallones, central California, is excellent. In light of environmental changes and the little-known influences and interactions of anthropogenic factors, however, the long-term future is uncertain.

## INTRODUCTION

Five species of pinniped reproduce, haul-out or migrate through the Gulf of the Farallones in central California (Bonnell et al. 1983, Allen 1994). These include California sea lion (*Zalophus californianus*), northern sea lion (*Eumetopias jubatus*), northern fur seal (*Callorhinus ursinus*), northern elephant seal (*Mirounga angustrirostris*) and Pacific harbor seal (*Phoca vitulina richardsi*). The abundance of each species in this region varies with both intrinsic population processes and extrinsic forces, such as variation in oceanographic conditions. Both Pacific basin-wide (e.g., El Niño Southern Oscillation) and local (e.g., sea temperature) physical and biological oceanic processes may influence the abundance of pinnipeds in central California. It has been hypothesized that prey availability is the likely proximate mechanism influencing pinniped distribution and abundance during large-scale oceanographic anomalies (e.g., Barber and Chavez 1983, Trillmich and Ono 1991).

Pinnipeds in central California require terrestrial habitat for hauling-out (i.e., resting) and reproduction. From various shore-based sites in the Gulf of the Farallones, we have conducted censuses of haul-outs and breeding colonies to investigate trends and oceanographic correlates of pinniped populations in the region over a 22-year period, 1973 to 1994. This time-series provides insight into the recovery, or lack thereof, of these species since enactment of the Marine Mammal Protection Act of 1972.

## STUDY AREA AND METHODS

The Gulf of the Farallones (GOF) is part of the California Current ecosystem, widely recognized as one of the most productive marine environments of the world. Hydrographic processes vary seasonally, including a period of intense coastal upwelling and advection occurring from February through July each year. Oceanic mixing during the late winter months of February and March may be especially important to the development of a robust marine food web in the region each year (Sydeman and Ainley 1994, Ainley et al. 1995). The timing and frequency patterns of coastal upwelling in the GOF varies annually, due, in part, to the influence of the El Niño Southern Oscillation (ENSO) and variation in the intensity and distribution of the Aleutian low pressure system in the Gulf of Alaska (Ainley et al. 1995). These basin-wide oceanographic events disrupt the development of robust food webs in the GOF, affecting both marine mammals and other upper trophic level marine predators (Bence et al. 1992).

We studied pinniped populations at the South Farallon Islands (SFI), Point Reyes (PR) and Double Point (Fig. 1). The SFI and PR are separated by approximately 30 km of coastal ocean habitat. The SFI are situated on the edge of the continental shelf, thereby affording pinnipeds relatively quick access to deep ocean waters. PR juts out into the ocean from the mainland. This coastal promontory is indirectly responsible for a persistent plume of upwelled water which develops off this section of coastline and often encircles the SFI. Double Point, located ~25 km south of the Point Reyes headlands, is a large pocket beach isolated by two small coastal promontories. All of these locations are under federal protection: the SFI are protected as the Farallon Islands National Wildlife Refuge under the jurisdiction of the U.S. Fish and Wildlife Service; Point Reyes and Double Point are protected as the Point Reyes National Seashore and are managed by the U.S. National Park Service.

Our study species include California sea lions, northern (or Steller) sea lions, northern elephant seals, and harbor seals. Although fur seals (both northern and Guadalupe) were recorded on the SFI during the study period, these species were omitted from analyses because of infrequent observations. At the SFI, we surveyed pinnipeds weekly (usually on Thursdays) between 1000-1600 hrs throughout the year. We conducted between 40 and 53 censuses annually (PRBO unpublished data). We counted pinnipeds hauled-out on the island from a vantage point located atop Lighthouse Hill at an elevation of 110 m (Fig 2a) and by visiting accessible beaches and haul-outs during times of the year when these areas were open to human visitation (roughly 15 August through 15 March). Animals were tallied with various age/size classes, although only a portion of these data are presented in this report.

During the winter, northern elephant seals breed on both the SFI and at PR (Huber 1987, Allen et al. 1989, Huber et al. 1991, Sydeman et al. 1991, Stewart et al. 1994). By observing tagged and/or individually marked females and censusing rookeries, we estimated the number of pups born each year at each sub-colony. We use this information as an index of the breeding population size each year. During spring, we also estimated the number of harbor seal pups born at Double Point. We also counted adult harbor seals at least 5 times at Double Point during the peak of the breeding season each year (late April-early May).

We used the maximum count of each species each year and the total number of annual births for northern elephant and harbor seals to assess population trends. To investigate changes in pinniped abundance through time, we fit an exponential model by regressing log-transformed ($\log_e$) abundance estimates against year. We then converted exponential rates to finite (i.e., annual) rates of increase using the formulae $e^r = \lambda$ (Caughley 1977, see Stewart 1992 and Barlow et al. 1993 for examples). The coefficient of determination ($R^2$) is reported to assess whether an exponential model fit the data for each species at each location reasonably well.

To investigate oceanographic correlates of pinniped abundance, we correlated log-transformed ($\log_e$) annual maxima with monthly values (October through May) of three oceanographic variables: sea surface temperature (SST), Bakun's Upwelling Index (Bakun 1975, UI) and sea level (SL) measured at San Francisco, California. We measured SST daily at the SFI and collated UI and SL data from National Oceanic and Atmospheric Administration (NOAA)/Pacific Fisheries Environmental Group (PFEG) oceanographers. This effort was undertaken as an exploratory "data-mining" analysis. We used multiple testing of monthly oceanographic parameters to narrow down the selection of variables to be included in subsequent multiple regression analyses (see below). We recognize that multiple testing can be problematic because the probability of falsely detecting a trend or correlation increases with the number of tests performed. Thus, the reported p-values should be considered approximations. More explicitly, p-values for initial correlations should be interpreted with caution. Next, we developed a multiple regression model for each species. We selected the month with the highest correlation coefficient for each oceanographic variable and entered these simultaneously in each model. In addition, time, represented by year, was included to account for population trends. In this manner we investigated whether there were significant relationships between pinniped abundance and oceanographic variables after controlling for overall species-specific population trends for each location.

California sea lion. - California sea lions haul-out on the SFI year-round; production has been limited to few (< 20) pups over the past two decades. California sea lion abundance at the SFI has increased significantly with time at an average rate of 6.4% per year from 1973 to 1994 (Fig. 2a; $b_1$(i.e., regression coefficient)=0.062, t=3.59, P=0.002, $R^2$=.39). Peak abundance (~7000 individuals) observed in 1984, followed the 1983 ENSO event. Omitting sea lion abundance data from 1983 and 1984 did not change the overall estimate of population growth ($b_1$=0.062, t=4.29, P<0.001, $R^2$=.51). The effect of ENSO events on California sea lion abundance at the SFI was reflected by significant positive relationships between numbers present and March sea surface temperature (SST) (Table 1; Fig. 2b) and April sea level (SL) (Table 1, Fig. 2c). This latter correlation was due only to high sea level during the 1983 ENSO. If this year is omitted from the analysis, the relationship between sea level and sea lion abundance was insignificant (P>0.10). We found no relationship between the Upwelling Index (UI) and California sea lion abundance. A multiple regression investigating the variables March SST, March UI, April sea level, and year revealed that none of the oceanographic measurements were significantly related to sea lion abundance when controlling for year (Table 2).

Northern sea lion. - Northern sea lions are present year-round in the Gulf of the Farallones, although numbers on the SFI are considerably greater during the breeding season lasting from

May through July each year. Historically, northern sea lions are known to have bred at PR, but have not done so since the mid 1970's (Chan 1979). At the SFI, northern sea lion abundance has varied considerably over the 22-yr study period (Fig. 3a) with an overall insignificant decline of -1.2% per annum ($b_1$=-0.012, t=-1.74, P=0.098, $R^2$=.14). Omitting the data from 1973 (an outlier) resulted in a decline of -1.4% per year ($b_1$=-0.014, t=-2.09, P=0.050, $R^2$=.19). The abundance of northern sea lions was significantly correlated with the October UI (Table 1, Fig. 3b) and February SL (Table 1, Fig. 3c). A multiple regression investigating the variables year, May SST, October UI, and February SL revealed a significant positive relationship between maximum numbers and the October UI (Table 2). The abundance of female northern sea lions at the SFI declined at an average rate of 2.9% per year (Fig. 4a; $b_1$=-0.029, t=-4.63, P<0.001, $R^2$=.64). The female population was greatest in 1977. Notably, during the last 6 years the abundance of cows fluctuated widely. The abundance of females was significantly negatively correlated with May SST (Table 1; Fig. 4b); there were fewer females on the SFI in years when May SST was elevated. In addition, there was a positive correlation with the May UI (Table 1; Fig. 4c). A multiple regression including the variables May SST, May UI, May SL, and year revealed that in the presence of year none of these oceanographic measurements were significantly related to the abundance of northern sea lion females at the SFI (Table 2).

Natality rates of northern sea lions also declined during the study period. Twenty to thirty pups were born annually in the late 1970s and early 1980s, compared with only 5 to 10 pups per year in recent time (Fig. 5).

The PR colony has been represented by <25 animals annually since the mid 1970's and no reproduction presently occurs at this location.

Pacific harbor seal. - Harbor seals are present year round in the Gulf of the Farallones; breeding occurs between March and June (Allen et al. 1989a). The abundance of harbor seals at the SFI and Double Point increased significantly throughout the study period, although patterns of increase were different at each location. At the SFI, numbers of harbor seals peaked in 1983, levelled off and then began to increase again displaying an overall increase of 10.4% per annum over the 22-yr period (Fig. 6a; $b_1$=0.099, t=10.48, P<0.001, $R^2$=.86). Abundance of harbor seals at the SFI also was positively correlated with March SST (Table 1; Fig. 6b), negatively correlated with May UI (Fig. 6c), and positively correlated with May SL (Fig. 6d). A multiple regression including the variables March SST, May UI, May SL and year revealed a positive relationship with March SST (Table 2). Together, year and March SST explained ~90% of the variation in harbor seal numbers at the SFI. Few (<10) harbor seal pups have been born on the SFI during the past 22 years.

At Double Point, maximum annual harbor seal abundance increased and then leveled off during the study period (Fig. 7a). The population grew at 8.7% per year from 1976 to 1987 ($b_1$=0.083, t=4.46, P=0.001, $R^2$=.67), before stabilizing thereafter ($b_1$=-0.021, t=1.59, P=0.164, $R^2$=.30). We also found a positive correlation between November SL and harbor seal numbers at Double Point (Table 1; Fig. 7b). A multiple regression including the variables year, May SST, May UI, November SL indicated that no oceanographic variables were correlated with the Double Point harbor seal abundance after controlling for year (Table 2).

The number of harbor seal births at Double Point increased at an overall rate of 5.2% per annum throughout the study period (Fig. 7c; $b_1$=0.051, t=6.08, P<0.001, $R^2$=.69).

Northern elephant seal. - Northern elephant seals are present year-round in the Gulf of the Farallones, but are most abundant during the spring molt or the fall juvenile haul-out period (Le Boeuf and Laws 1994, PRBO unpublished data). Maximum counts of northern elephant seals at the SFI increased at 29.1% per year (Fig. 8a; $b_1$=0.255, t=11.99, P<0.001, $R^2$=.97) between 1973 and 1978. Following 1978, the population has been growing slowly at <1% per year ($b_1$=0.006, t=1.77, P=0.096, $R^2$=.17). Peak numbers fluctuated between 800 and 1000 animals each year. We found significant correlations between maximum elephant seal abundance at the SFI and January SST and May SL (Table 1, Figs. 8b and 8c, respectively). A multiple regression including the variables year, January SST, May UI, and May SL revealed a positive relationship with January SST after controlling for year (Table 2). Together, year and January SST explained ~75% of the variation in maximum elephant seal numbers at the SFI.

Northern elephant seals colonized the SFI as a breeding colony in 1972 (Le Boeuf et al. 1974, Stewart et al. 1994). The number of births each year increased significantly until 1983, following a pattern of exponential growth. From 1973 to 1983, the numbers of pups born increased at an average rate of 56.5% per annum (Fig. 9a; $b_1$=0.448, t=7.08, P<0.001, $R^2$=.85). Between 1983 and 1994, however, the number of pups produced on the SFI declined by an annual rate of 3.3% per year ($b_1$=-0.032, t=-4.973, P<0.001, $R^2$=.71). In 1983, a peak of 475 pups were born, while in recent years numbers of pups have fluctuated between 300-400.

Northern elephant seals colonized PR in 1981 (Allen et al. 1989b). The colony has grown constantly since its inception, displaying an annual rate of increase of 50.2% per year (Fig. 9b; $b_1$=0.407, t=12.61, P<0.001, $R^2$=.93). We did not have a sufficient continuous-year sample of maximum elephant seal numbers during the spring molt or fall haul-out period for PR to permit statistical analysis.

## DISCUSSION

Historically, pinniped populations in the Gulf of the Farallones were exploited for fur, oil, and meat and many animals were killed due to their interactions with commercial fisheries (Scammon 1874, Ainley and Lewis 1974, Bonnell et al. 1983, Lowry et al. 1992, Barlow 1994). With enactment of protective measures including the Marine Mammal Protection Act of 1972, the Endangered Species Act of 1973 (U.S. Public Law 93-205), and protected status for terrestrial habitats (i.e., Farallon National Wildlife Refuge and Point Reyes National Seashore) where these animals rest and reproduce, some of these populations have recovered. The data presented herein for California sea lions, harbor seals, and northern elephant seals show substantial increases in abundance over the past two decades. Despite protection, however, the northern sea lion population is declining, and the northern fur seal population, which may have numbered 50,000 on the SFI in the late 1700's/early 1800's (Ainley and Lewis 1974) has not recovered (PRBO unpublished data).

California sea lion. - Between 1973 and 1994, California sea lion abundance on the SFI increased at roughly 6% per annum. Estimates of the state-wide population increase based on pup production at breeding colonies range from 5-8% per year over the past two decades (DeMaster et al. 1982, Lowry et al. 1992, Barlow et al. 1995). Although populations are growing, interactions with commercial fisheries may continue to limit the rate of population increase. Barlow et al. (1994) estimated that entanglement in set and drift nets is responsible for the mortality of thousands of animals each year. California sea lions at the SFI increased during the 1983 and 1992 ENSOs due, in part, to a general migration northward from southern California breeding grounds, movements which were associated with poor food availability in the Southern California Bight (Trillmich and Ono 1991).

Northern sea lion. - In contrast to the other species investigated, northern sea lion populations have declined in the Gulf of the Farallones and throughout their range in California and Oregon (Le Boeuf et al. 1991, Loughlin et al. 1992). In 1990, northern sea lions were listed as a threatened species under the Endangered Species Act of 1973, mainly because of substantial declines in southwestern Alaska (Merrick et al. 1987, NMML 1985); they are presently being considered for up-listing to endangered for the southwestern Alaska region (Federal Register 1994). Under the ESA, two "vertebrate populations" of northern sea lions are recognized. The California and Oregon animals are lumped with the population centered in SE Alaska. The latter region supports an apparently stable population (Loughlin 1992, NMML 1995). It is unknown, though doubtful, that the California and SE Alaska populations are demographically linked via immigration because one population is declining and the other is apparently stable. Therefore, considering the SE Alaska, British Columbia, Oregon and California populations as one metapopulation (defined as a group of interacting sub-populations) appears problematic. Instead, for management purposes, distinguishing the Oregon and California population from that of SE Alaska and British Columbia makes sense given contrasting population trends. Oceanographically, this distinction also would separate animals associated with the California Current marine ecosystem (from Point Conception in southern California @ 35° N to the northwestern tip of Washington @ 48° N) from those associated with other portions of the North Pacific Gyre. Management efforts and applied studies, particularly those related to forage reserves, effects of food availability on the demography, and disease, could then focus on distinct ecosystems with differing oceanic characteristics and anthropogenic pressures.

In California, the decline of northern sea lions on the SFI (3% p.a.) and at Año Nuevo Island (Le Boeuf et al. 1991) is comparable, though less in absolute terms, than the decline (8% p.a.) in southwestern Alaska (NMML 1995). For southwestern Alaska, the NMML (1995) hypothesized that chronically reduced juvenile survival, coupled with acute mortality of adults early in the period of decline, was responsible for the observed population change. Disease and changes in prey availability are believed to be the likely mechanisms reducing juvenile survival in southwestern Alaska. Similarly, there appear to be several factors which are likely to be affecting population parameters of northern sea lions in California. First, a general warming trend of the ocean may have affected characteristics of the California Current food web, thereby reducing northern sea lion prey availability (e.g. Sydeman and Ainley 1994, Roemmich and McGowan 1995). The greatly expanded California sea lion population also may be playing a role by competing with northern sea lions for prey. Long-term changes in their prey base could

be responsible for the observed poor natality rates in the SFI population (see also Huber 1984). Unfortunately, we have no data on juvenile or adult survival for the central California population with which to investigate demographic processes and hypotheses concerning the effects of food availability on population dynamics. Second, there is considerable evidence that contaminants and disease and possible interactions between these factors may be influencing natality rates and reproductive success. At the SFI premature stillbirths accounted for 20-65% of pup mortality between 1973 and 1983 (Huber 1984), and in each year only a small proportion (~< 10%) of the SFI female populations give birth each year. Viral and bacterial diseases, such as San Miguel Sea Lion virus and *Leptospira*, *interogans*, *serovar*, *pomona*, respectively, and a diverse array of pollutants (i.e., DDE, PCBs, Hg and Cu; Huber 1984, Jarman et al. 1996, Sydeman 1996) may be related to both premature parturition and low natality rates. Third, small populations often demonstrate substantial variability in demographic attributes. Our data on the population of female sea lions and irregularities in reproduction may indicate that this population is being affected by its small population size manifested by demographic stochasticity (see Burgman et al. 1993).

In conclusion, we believe that population of northern sea lions south of 48° N should be considered a separate "vertebrate population" and recommend that this distinct population be considered endangered under the ESA. Moreover, as numerous populations in California have declined precipitously (e.g. Año Nuevo Island, Le Boeuf et al. 1991, Ono 1992), or are extirpated (e.g. San Miguel Island, Antonelis and Fiscus 1980, NMML 1995), investigations to determine the causes of population decline should be given top priority.

Pacific Harbor seal. - The Gulf of the Farallones harbor seal population has grown considerably, as it has throughout much of the eastern North Pacific Ocean south of the Gulf of Alaska at approximately 5-8% per year (Allen et al. 1989a, Beeson and Hanan 1994, Huber et al. 1994). At the SFI, a marked peak in harbor seal abundance occurred in 1983, corresponding with the exceptionally strong ENSO event during that year. We did not find a similar trend at PR. We believe that this trend may be explained by poor food availability, which may have forced seals to leave their traditional neritic foraging grounds in search of food in more pelagic waters. Similarly Brown and Mate (1983) hypothesized that harbor seals in Oregon moved from coastal to estuarine habitats in search of food under poor foraging conditions. Moreover, the increase in abundance on the SFI must be the result of immigration rather than recruitment as the small number of offspring produced at the SFI could not account for the observed levels of population increase (Allen et al. 1989a).

Northern elephant seal. - The increased abundance of northern elephant seals in the Gulf of the Farallones is likely a reflection of their recovery from near extinction resulting from protection afforded this species by laws passed by the United States and Mexican governments in the early 20th century and the Marine Mammal Protection Act (Le Boeuf et al. 1974). Northern elephant seal populations in California are expanding at ~8-14% per year (Cooper and Stewart 1983, Stewart 1992, Stewart et al. 1994); rates of increase have generally decreased in recent years. Associated with this increase has been range expansion and the (re)colonization of mainland beaches in central (Allen et al. 1989) and northern California (Jacques and Strong 1995) and Oregon (J. Hodder. Oregon Institute of Marine Biology, pers. comm.). In relation to

productivity, the SFI colony appeared to reach carrying capacity by 1983 and is now displaying a decline, whereas populations at other, newer locations continue to grow. The PR colony has been growing exponentially, and while there have been distributional shifts in the locations of animals on the Point Reyes (Allen 1995), there appears to be ample habitat to support a considerably larger breeding population. There were also greater numbers of elephant seals in years when mean January SST was higher.

On the SFI, the availability of and access to breeding habitat appears to have diminished and influenced the northern elephant seal breeding population. Up until 1983, the principle breeding area on the SFI was a beach known as Sand Flat. This colony had three access points, one through another breeding area (Mirounga Beach) and two through surge channels. Prior to 1983, each of these access routes was characterized by sloping sand leading to rock. During the winter of 1983, however, large swells associated with severe storms, washed the majority of sand off Sand Flat and out of 2 of the 3 access routes. Access to Sand Flat through these surge channels is now blocked by small (~2m) cliffs that are difficult for pregnant females to negotiate. Coincident with these habitat changes, there has been a substantial decline of breeding cows on Sand Flat, from a peak of ~180 in 1983 to less than 60 in 1994 (PRBO unpublished data). Many marked (i.e., tagged) animals moved from Sand Flat to another sub-colony, known as Shell Beach, and others were recorded on Point Reyes (PRBO and PRNS, unpublished data). Shell Beach appeared to become saturated by 1986, and has also sustained moderate declines in recent years. Consequently, we believe that habitat changes, mostly those associated with loss of sand and deterioration of access routes, coupled with crowding, have been primarily responsible for the decline in the SFI northern elephant seal population in recent years.

Other factors that may be playing a role in the decline of northern elephant seal on the SFI include predation by white sharks (*Carcharodon carcharias*) and bycatch in commercial drift and set-net fisheries (Barlow et al. 1994). Of these factors, incidental take in fisheries is not thought to play a strong role in elephant seal population dynamics (Barlow et al. 1994); however, predation on juvenile elephant seals hauled out on the SFI during fall each year has increased through time (Ainley et al. 1985, Pyle et al. 1996). It is possible that current levels of shark predation are limiting recruitment into the SFI population.

Conclusion. - The short-term prognosis for pinniped populations in the Gulf of the Farallones, with the exception of the northern sea lion, is excellent. Protective measures (i.e., the Marine Mammal Protection Act and Endangered Species Act and designation of preserves) have been sufficient to enable some populations to recover. However, interdecadal variability in the California Current marine ecosystem has only recently been recognized (Roemmich and McGowan 1995) and the long-term influence of these patterns on pinniped population dynamics has yet to be assessed. Moreover, although interannual variability in marine conditions (e.g. ENSO events) did not appear to have detrimental effects on the recovery of California sea lions, and harbor and northern elephant seals, the frequency of events appears to have increased in recent time (Quinn et al. 1987). We suspect that when pinniped numbers approach carrying capacity, the effects of ENSO and similar events on pinniped populations may become more apparent. Lastly, during the past 20 years the California marine environment has been subjected to both increasing and decreasing anthropogenic pressures from commercial fishing activities

and the introduction of pollutants. In light of environmental uncertainty and the little-known influences and interactions of anthropogenic factors, the long-term future of pinniped populations in the Gulf of the Farallones cannot be accurately predicted.

## ACKNOWLEDGEMENTS

Funding for this report was provided by the NOAA/National Marine Fisheries Service, Southwest Fisheries Science Center under contract no. 40JGNF500431 to WJS, Exxon Corporation, Homeland Foundation, Gellert Foundation, Roberts Foundation, and Point Reyes National Seashore. PRBO biologists R. Boekelheide, H. Carter, S. Emslie, H.R. Huber, R. LeValley, J. Lewis, E. McLaren, S. Morrell, S. Johnston, J. Nusbaum, T. and J. Penniman, P. Pyle, and J. Walsh and numerous volunteers participated in weekly censuses of pinnipeds at the SFI. We thank the U.S. Fish and Wildlife Service, managers of the Farallon National Wildlife Refuge for partial funding to conduct fieldwork and encouragement with these studies. Over the years, financial support was provided by the Marine Mammal Commission, National Marine Fisheries Service/Southwest Fisheries Center, Gulf of the Farallones and Cordell Bank National Marine Sanctuaries, Point Reyes Bird Observatory, National Park Service, Homeland Foundation, Bradford Foundation, Roberts Foundation, Gellert Foundation, Exxon Corporation and Friends of the Farallones. We thank the Farallon patrol for transportation to and from Southeast Farallon Island. J. Barlow and M. Lowry reviewed an earlier draft of this report. This is PRBO contribution no. 735.

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Table 1. Correlation coefficients between $\log_e$ maximum counts of pinnipeds in the Gulf of the Farallones each year and environmental variables: mean monthly sea surface temperature (SST) measured at the South Farallon Islands (SFI), Bakun's upwelling index (UI), and sea level (SL) measured at San Franscisco. See text for further details.

A. California sea lions (*Zalophus californianus*) at the SFI.

| Variable | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May |
|---|---|---|---|---|---|---|---|---|
| SST[a] | .16 | .22 | .27 | .37 | .35 | .45* | .42* | .32 |
| UI[b] | .06 | .01 | -.18 | .26 | .06 | -.35 | -.21 | -.18 |
| SL[c] | .15 | .33 | .40 | .26 | .10 | .39 | .52* | .44 |

B. Northern sea lions (*Eumetopias jubatus*) at the SFI.

| Variable | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May |
|---|---|---|---|---|---|---|---|---|
| SST[a] | -.31 | -.26 | -.08 | -.10 | -.14 | -.36 | -.29 | -.39 |
| UI[b] | .71* | .02 | .02 | .18 | .62* | .01 | .19 | .34 |
| SL[c] | -.36 | -.29 | -.21 | .38 | -.57* | -.29 | -.17 | -.34 |

C. Northern sea lion (*Eumetopias jubatus*) females at the SFI.

| Variable | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May |
|---|---|---|---|---|---|---|---|---|
| SST[a] | -.15 | -.09 | -.04 | -.10 | -.05 | -.35 | -.37 | -.53* |
| UI[b] | .35 | -.24 | .02 | .00 | .20 | .07 | .15 | .52* |
| SL[c] | -.15 | -.13 | -.05 | .17 | -.17 | -.05 | -.10 | -.28 |

D. Harbor seals (*Phoca vitulina*) at the SFI.

| Variable | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May |
|---|---|---|---|---|---|---|---|---|
| SST[a] | .11 | .23 | .29 | .48* | .42* | .54* | .52* | .53* |
| UI[b] | -.22 | .19 | -.19 | -.33 | -.17 | -.27 | -.29 | -.47* |
| SL[c] | .18 | .32 | .36 | .22 | .26 | .35 | .45 | .68* |

E. Harbor seals (*Phoca vitulina*) at Point Reyes.

| Variable | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May |
|---|---|---|---|---|---|---|---|---|
| SST[d] | .12 | .30 | .38 | .29 | .11 | .27 | .40 | .41 |
| UI[e] | -.36 | -.15 | -.14 | -.11 | .01 | -.32 | -.19 | -.37 |
| SL[f] | .40 | .53* | .48* | -.02 | .05 | .31 | .31 | .46* |

F. Northern elephant seals (*Mirounga angustrirostris*) at the SFI.

| Variable | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May |
|---|---|---|---|---|---|---|---|---|
| SST[a] | -.06 | .07 | .22 | .49* | .34 | .43* | .47* | .37 |
| UI[b] | .11 | .17 | -.28 | -.28 | .07 | -.29 | -.27 | -.33 |
| SL[c] | -.01 | .10 | .18 | .17 | .07 | .23 | .36 | .52* |

[a] n=22 years, [b] n=21, [c] n=18, [d] n=19, [e] n=18, [f] n=15

* $P<0.05$

Table 2. Results of multiple regression analyses investigating the relationship between pinniped abundance in the Gulf of the Farallones, California and environmental conditions. Estimates of maximum pinniped population size were $\log_e$ transformed prior to analysis. Monthly mean values of oceanographic variables were selected based on the simple correlations presented in Table 1. See text and Table 1 for abbreviations.

A. California seal lions at the SFI: $F_{4,13}=3.01$, $P=0.059$, $R^2=.48$

| Variable | Coeff. + s.e. | t-value | p-value |
|---|---|---|---|
| Year | 0.056±0.026 | 2.14 | 0.052 |
| March SST | 0.093±0.147 | 0.64 | 0.536 |
| March UI | -0.000±0.003 | -0.02 | 0.981 |
| April SL | 0.003±0.002 | 1.14 | 0.274 |
| Constant | -5.304 | | |

B. Northern seal lions at the SFI: $F_{4,13}=5.23$, $P=0.010$, $R^2=.62$

| Variable | Coeff. + s.e. | t-value | p-value |
|---|---|---|---|
| Year | 0.002±0.007 | 0.24 | 0.816 |
| May SST | 0.006±0.061 | 0.10 | 0.919 |
| Oct. UI | 0.004±0.002 | 2.15 | 0.053 |
| Feb. SL | -0.001±0.000 | -1.83 | 0.092 |
| Constant | 6.841 | | |

C. Northern seal lion females at the SFI: $F_{4,13}=3.94$, $P=0.026$, $R^2=.55$

| Variable | Coeff. + s.e. | t-value | p-value |
|---|---|---|---|
| Year | -0.033±0.009 | -3.50 | 0.004 |
| May SST | -0.016±0.074 | -0.21 | 0.837 |
| May UI | -0.000±0.001 | -0.37 | 0.718 |
| May SL | 0.001±0.001 | 0.50 | 0.628 |
| Constant | 6.150 | | |

D. Harbor seals at the SFI: $F_{4,13}=28.89$, $P<0.001$, $R^2=.90$

| Variable | Coeff. ± s.e. | t-value | p-value |
|---|---|---|---|
| Year | 0.084±0.012 | 6.77 | <0.001 |
| Mar. SST | 0.158±0.062 | 2.56 | 0.024 |
| May UI | -0.000±0.001 | -0.13 | 0.990 |
| May SL | 0.002±0.001 | 1.40 | 0.185 |
| Constant | -9.961 | | |

E. Harbor seals at PR: $F_{4,10}=7.12$, $P=0.006$, $R^2=.74$

| Variable | Coeff. ± s.e. | t-value | p-value |
|---|---|---|---|
| Year | 0.052±0.014 | 3.84 | 0.003 |
| May SST | 0.075±0.094 | 0.80 | 0.445 |
| May UI | -0.001±0.001 | -0.54 | 0.599 |
| Nov. SL | 0.001±0.001 | 1.31 | 0.221 |
| Constant | -1.523 | | |

F. Northern elephant seals at the SFI: $F_{4,13}=9.36$, $P=0.001$, $R^2=.74$

| Variable | Coeff. ± s.e. | t-value | p-value |
|---|---|---|---|
| Year | 0.055±0.015 | 3.77 | 0.002 |
| Jan. SST | 0.173±0.073 | 2.38 | 0.033 |
| May UI | 0.001±0.001 | 0.76 | 0.463 |
| May SL | 0.001±0.001 | 1.12 | 0.281 |
| Constant | -4.318 | | |

## FIGURE LEGENDS

Figure 1. Map of the Gulf of the Farallones, California, showing locations of Point Reyes, Double Point, and the Farallon Islands. Studies of California and northern sea lions and harbor and elephant seals were conducted at the South Farallon Islands. Studies of northern elephant seals were conducted at Point Reyes and harbor seals were studied at Double Point.

Figure 2. Changes in the California sea lion population at the South Farallon Islands, 1973-1994, with (a) time, (b) March sea surface temperature (SST) and (c) variation in April sea level.

Figure 3. Changes in the northern sea lion population ($\log_e$ maximum numbers) on the South Farallon islands, 1973-1994, with (a) time, (b) upwelling in October and (c) February sea level. The regression lines apparent in (a) reflect analyses with (lower line) and without (upper line) 1973.

Figure 4. Changes in the female northern sea lion population ($\log_e$ maximum numbers) on the South Farallon islands, 1973-1994, with (a) time, (b) May sea surface temperature (SST) and (c) upwelling in May.

Figure 5. Changes in the female northern sea lion population and natality rates on the South Farallon Islands, 1974-1994.

Figure 6. Changes in the harbor seal population ($\log_e$ maximum numbers) on the South Farallon Islands, 1973-1994, with (a) time, (b) March sea surface temperature (SST), (c) upwelling in May, and (d) May sea level.

Figure 7. Changes in the harbor seal population ($\log_e$ maximum numbers) at Double Point, 1976-1994, with (a) time, and (b) November sea level. Figure 7 (c) reflects changes in the natality of harbor seals ($\log_e$ number births) at Double Point.

Figure 8. Changes in the northern elephant seal population ($\log_e$ maximum numbers) on the South Farallon Islands, 1973-1994, with (a) time, and (b) January sea surface temperature (SST) and (c) May sea level.

Figure 9. Changes in the natality ($\log_e$ number births) of northern elephant seals on (a) the South Farallon Islands, 1973-1994 and (b) Point Reyes, 1981-1994.

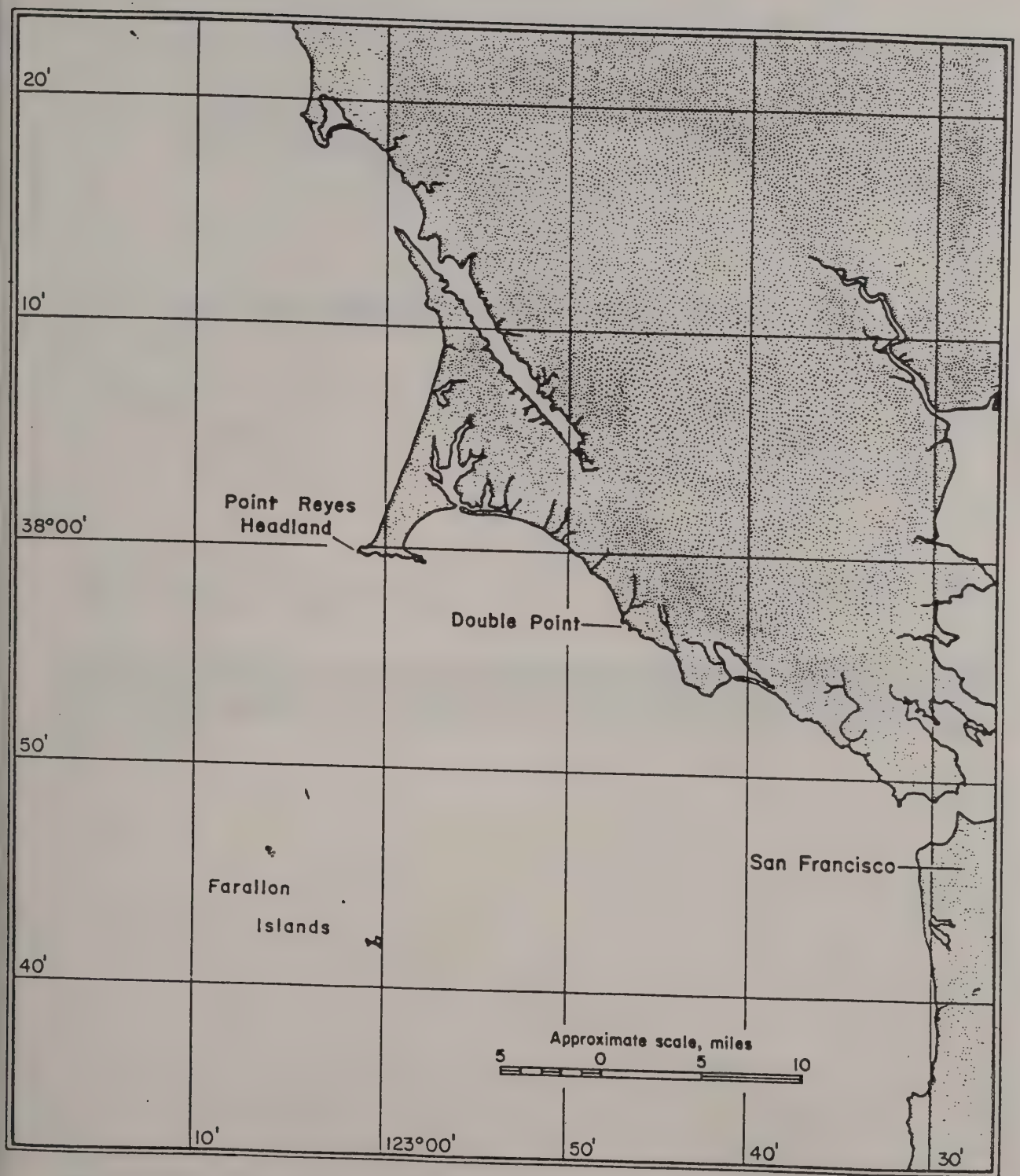


Figure 1. Map of the Gulf of the Farallones, California, showing locations of Point Reyes, Double Point, and the Farallon Islands. Studies of California and northern sea lions and harbor and elephant seals were conducted at the South Farallon Islands. Studies of northern elephant seals were conducted at Point Reyes.

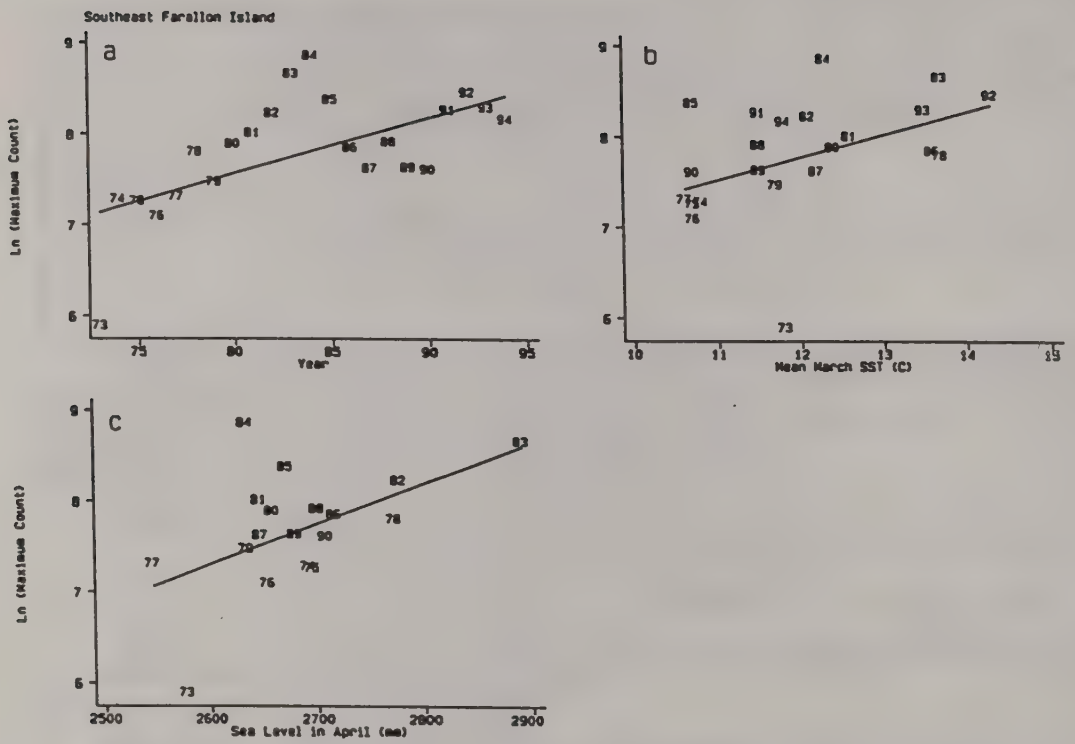


Figure 2. Changes in the California sea lion population at the South Farallon Islands, 1973-1994, with (a) time, (b) March sea surface temperature (SST) and (c) variation in April sea level.

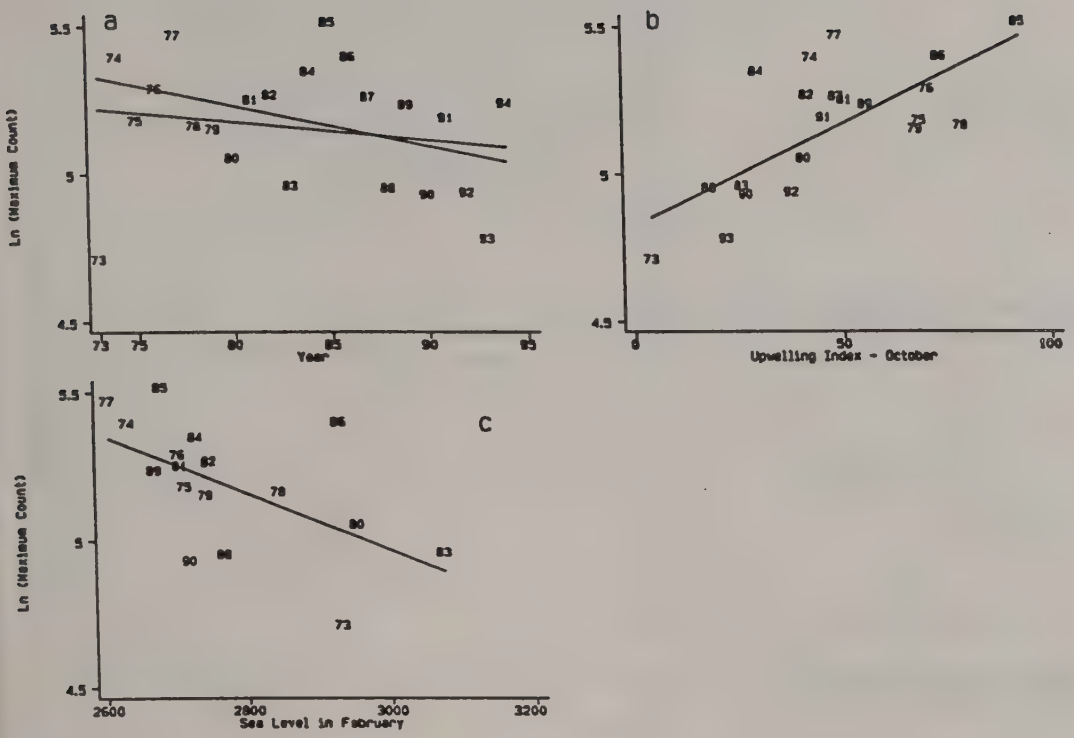


Figure 3. Changes in the northern sea lion population ($\log_e$ maximum numbers) on the South Farallon islands, 1973-1994, with (a) time, (b) upwelling in October and (c) February sea level. The regression lines apparent in (a) reflect analyses with (lower line) and without (upper line) 1973.

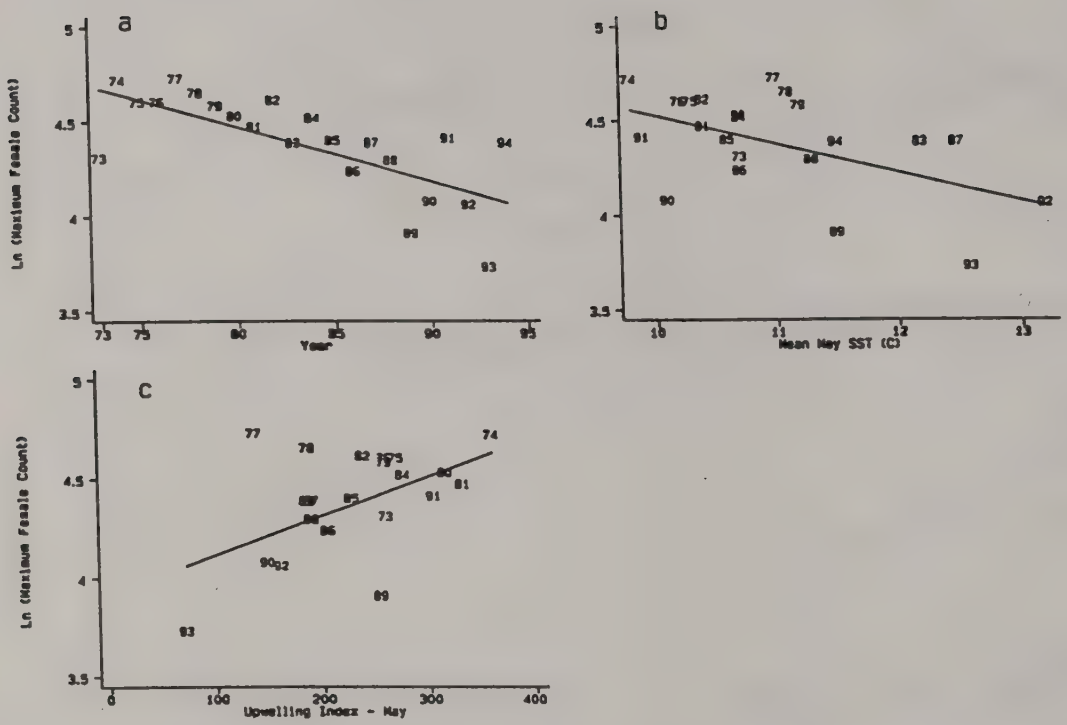


Figure 4. Changes in the female northern sea lion population ($\log_e$ maximum numbers) on the South Farallon islands, 1973-1994, with (a) time, (b) May sea surface temperature (SST) and (c) upwelling in May.

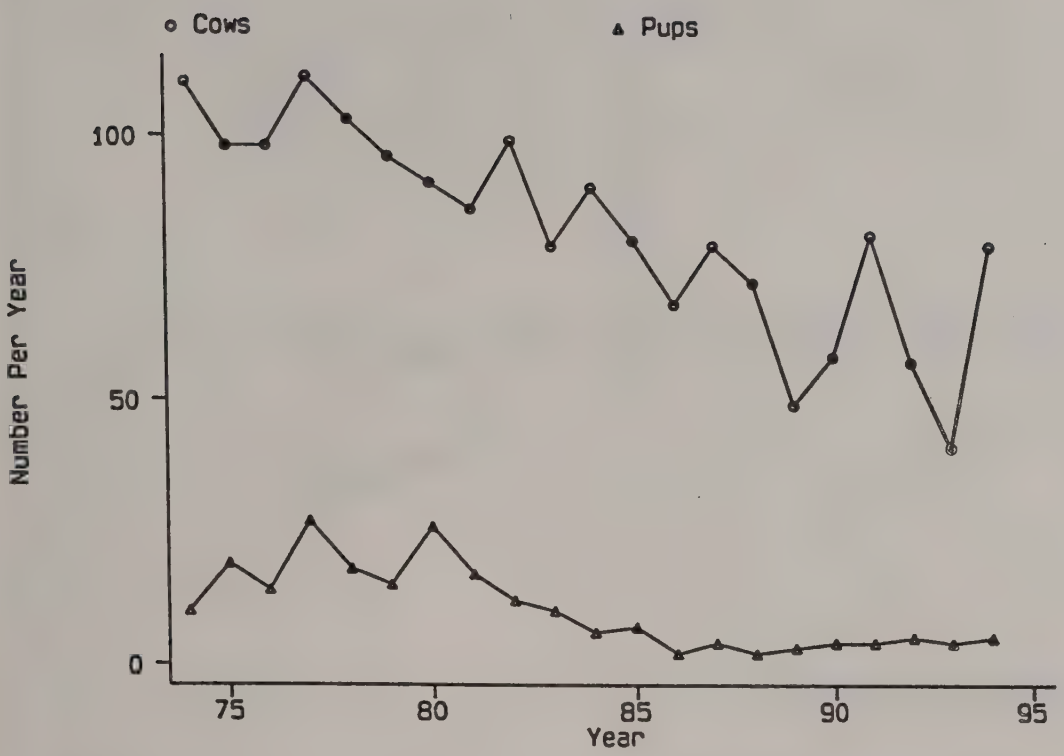


Figure 5. Changes in the female northern sea lion population and natality rates on the South Farallon Islands, 1974-1994.

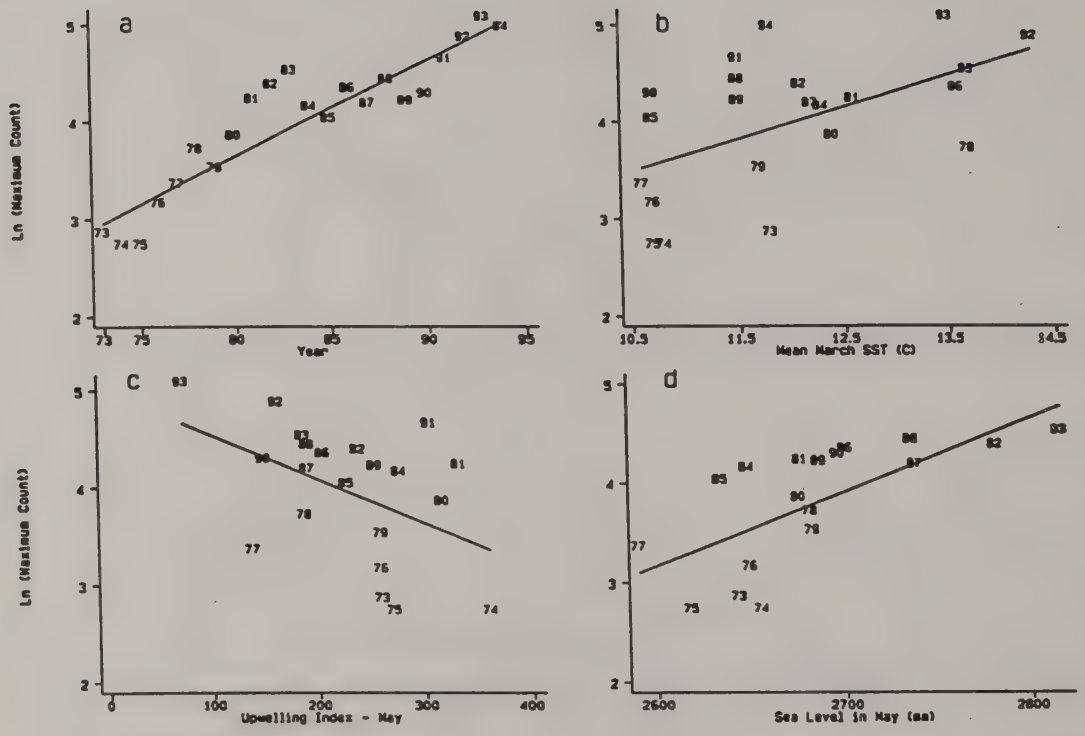


Figure 6. Changes in the harbor seal population ($\log_e$ maximum numbers) on the South Farallon Islands, 1973-1994, with (a) time, (b) March sea surface temperature (SST), (c) upwelling in May, and (d) May sea level.

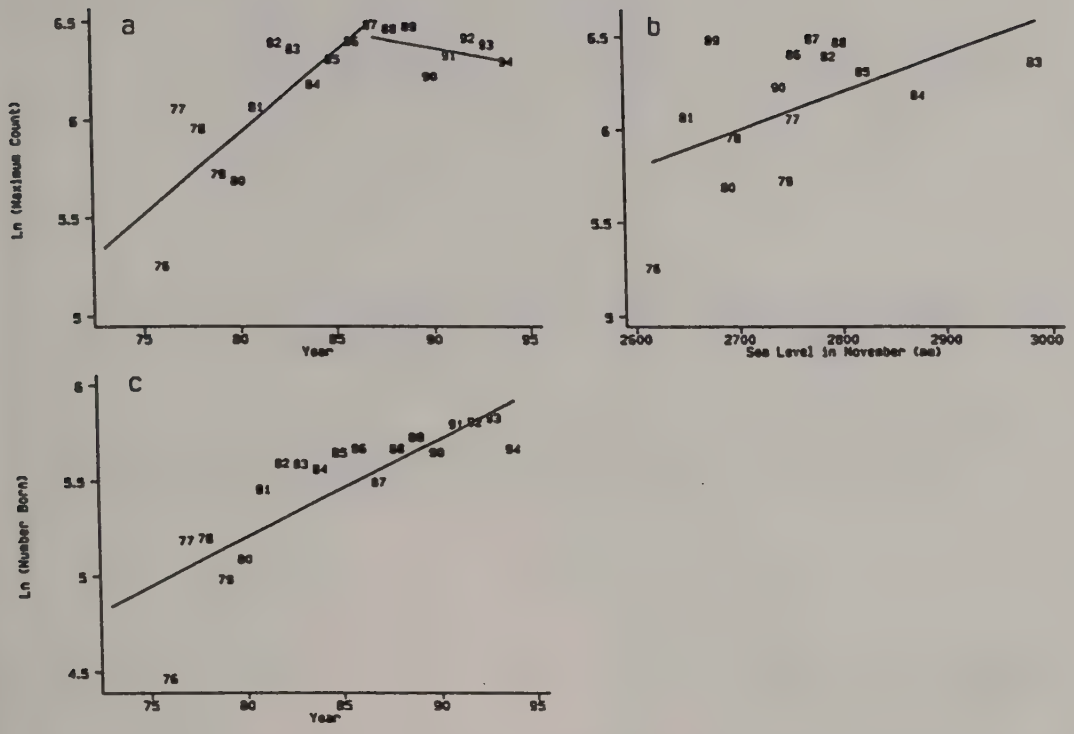


Figure 7. Changes in the harbor seal population ($\log_e$ maximum numbers) at Double Point, 1976-1994, with (a) time, and (b) November sea level. Figure 7 (c) reflects changes in the natality of harbor seals ($\log_e$ number births) at Double Point.

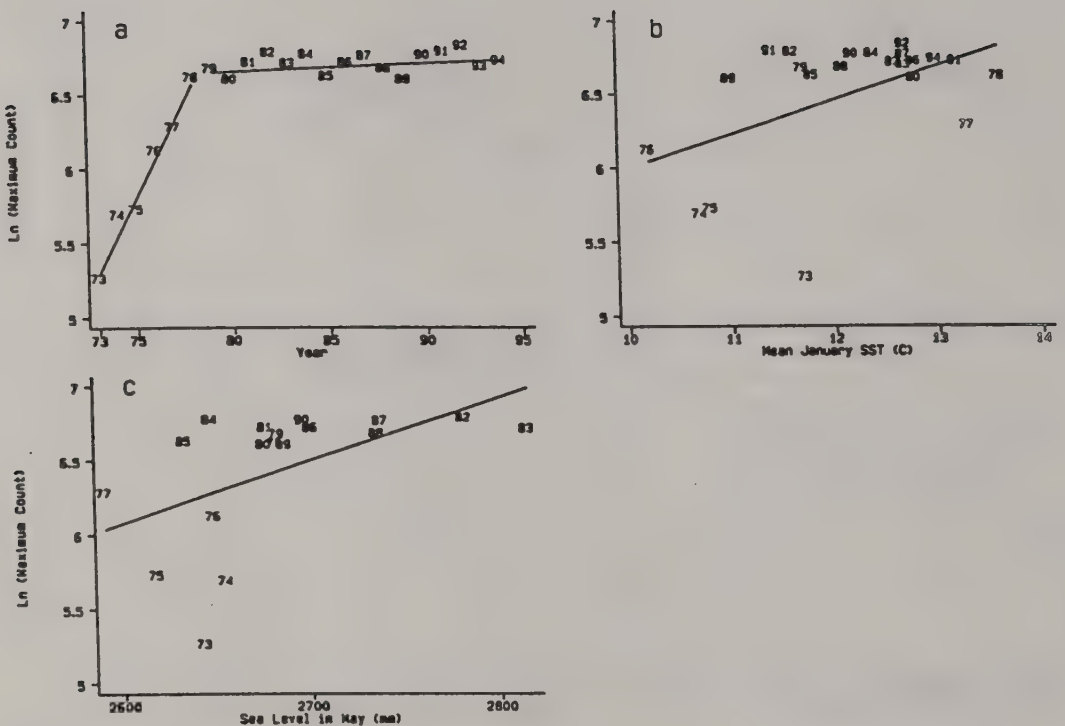


Figure 8. Changes in the northern elephant seal population ($\log_e$ maximum numbers) on the South Farallon Islands, 1973-1994, with (a) time, and (b) January sea surface temperature (SST) and (c) May sea level.

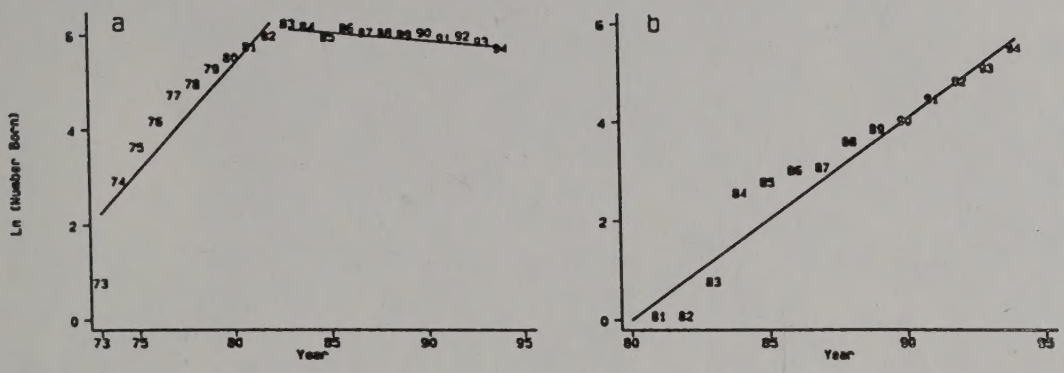


Figure 9. Changes in the natality ($\log_e$ number births) of northern elephant seals on (a) the South Farallon Islands, 1973-1994 and (b) Point Reyes, 1981-1994.